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Pollen Grain Size, Density, and Settling Velocity for Palmer Amaranth (*Amaranthus palmeri*)

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Palmer amaranth is resistant to several herbicides, including glyphosate, and there is concern that the resistance traits can be transferred between spatially segregated populations via pollen movement. The objective of this study was to describe the physical properties of Palmer amaranth pollen, specifically size, density, and settling velocity (V_s), that influence pollen flight. The mean diameter for Palmer amaranth pollen, as determined by light microscopy, was 31 μm (range of 21 to 38 μm); mean pollen diameter as measured with the use of an electronic particle sizer was 27 μm (range of 21 to 35 μm). The mean density of the solid portion of the pollen grain was 1,435 kg m^{-3}. Accounting for the density of the aqueous fraction, the mean density of a fully hydrated pollen grain was 1,218 kg m^{-3}. By Stokes's law, the estimated mean theoretical V_s for individual Palmer amaranth pollen grains was 3.4 cm s^{-1} for the range of pollen diameters with a mean of 31 μm and 2.6 cm s^{-1} for the range of pollen diameters with a mean of 27 μm. Results from laboratory studies indicated the majority of single pollen grains settled at a rate of 5.0 cm s^{-1}. The difference between the theoretical and empirical estimates of V_s was likely due to changes in pollen density and shape postanthesis, which are not accounted for using Stokes's law, as well as the presence pollen clusters.

Nomenclature: Glyphosate; Palmer amaranth, *Amaranthus palmeri* S.Wats.

Key words: Gene flow, herbicide resistance, pollen movement.

Palmer amaranth is an erect, annual, dioecious species of pigweed native to the southwestern United States and northern Mexico. Palmer amaranth has moved beyond its native range and invaded the midsouth and southeastern United States, where it is a significant weed of agricultural environments (Webster 2005). Palmer amaranth is extremely competitive with crops, reducing corn (*Zea mays* L.), soybean [*Glycine max* (L.) Merr.], peanut (*Arachis hypogaea* L.) and cotton (*Gossypium hirsutum* L.) yields up to 91% (Burke et al. 2007; Klingaman and Oliver 1994; Massinga et al. 2001; Morgan et al. 2001). Its competitiveness is due, in part, to its rapid growth rate. Under full sunlight, Horak and Loughin (2000) determined that Palmer amaranth plants grew at rates of 0.18 to 0.21 cm GDD^{-1} (growing degree days; base temperature of 10 C), which are 30 to 160% greater than those for common waterhemp (*A. rudis* Sauer), redroot pigweed (*A. retroflexus* L.), and tumble pigweed (*A. albus* L.). Palmer amaranth's growth rate is partly a function of its high rate of photosynthesis (80 μmol m^{-2} s^{-1}; Ehleringer 1983), which is approximately four times that of many row crops, including cotton (Ehleringer and Hammond 1987).

Trucco et al. (2005a) commented that under repeated herbicide exposure, the most significant adaptation a weed can evolve is herbicide resistance. In Georgia, Palmer amaranth populations have developed resistance to two classes of herbicides, acetolactate-synthase (ALS)–inhibiting herbicides and glyphosate (Culpepper et al. 2006; Heap 2008). As of 2007, five states (Arkansas, Kansas, North Carolina, South Carolina, and Tennessee), in addition to Georgia, have confirmed cases of ALS-resistant Palmer amaranth and five states (Arkansas, Georgia, North Carolina, South Carolina, and Tennessee) have biotypes resistant to glyphosate (Heap 2008; Norsworthy et al. 2008; Steckel et al. 2008). Palmer amaranth resistance to dinitroaniline herbicides has been documented in South Carolina (Gossett et al. 1992) and resistance to the photosystem II inhibitors has been reported in Kansas and Texas (Heap 2008). There are preliminary indications that the triazine herbicides may be ineffective against Palmer amaranth populations in middle Georgia (E. P. Prostko, personal communication).

Development of herbicide resistance in Palmer amaranth is a significant issue for the growers in the southern United States. Glyphosate-resistant cotton technology was rapidly adopted in the United States, accounting for greater than 97% of the cotton grown in southeastern United States [US Department of Agriculture, Agricultural Marketing Service (USDA-AMS) 2007]. The reason for this rapid adoption was a combination of simplified application procedures with glyphosate, improved weed control efficacy, and greater flexibility in target weed sizes (Duke and Powles 2008). Alternative management systems that include herbicides with soil residual activity against Palmer amaranth will increase costs two- to fourfold over glyphosate-only systems, and the success of these alternative systems depends upon timely rainfall or irrigation (Culpepper et al. 2008).

Herbicide resistance in weeds can either develop de novo or be acquired through gene flow, which is accomplished by the movement of pollen and seed (Jasieniuk et al. 1996). Because Palmer amaranth is dioecious, there is concern that the resistance trait can be transferred via wind-mediated pollen dispersal to remote, herbicide-sensitive populations. If the rate of gene flow exceeds the rate of mutation, which is generally accepted to be 10^{-6} gametes per locus per generation, and assuming single nuclear gene inheritance, the subsequent increase in the initial frequency of resistance genes will act to reduce the time required for a population to reach a specified resistance level once the herbicide is applied (Jasieniuk et al. 1996). Although the importance of gene flow, relative to genetic mutation, as a source of resistance is still unknown, it is accepted that interpopulation gene flow for outcrossing species occurs at rates that are evolutionarily significant (Ackerman 2000; Ellstrand and Schierenbeck 2000; Jasieniuk et al. 1996). Although most pollen grains settle close to the source plant, there is evidence indicating that long-distance dispersal events can and do occur (Alibert et al. 2005; Hanson

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et al. 2005; Luna et al. 2001; Massinga et al. 2003; Matus-Cadiz et al. 2004; Saeglitz et al. 2000).

Pollen grains of anemophilous (wind pollinated) species are typically small and smooth, and are more likely to be transported away from the paternal plant than larger, sticky, and/or ornamented grains (Ackerman 2000; Primack 1978). The length of time wind-dispersed pollen remains aloft is determined, in part, by the gravitational settling velocity of the grains in still air. The V_s for small (1 to ~100 μm) and round particles, such as pollen, can either be determined empirically with the use of a settling tower, or estimated with an application of Stokes's law:

$$V_s = \frac{1}{18} d^2 g \left(\frac{\sigma_p - \sigma_f}{\eta} \right), \quad [1]$$

where d is the diameter of the particle (cm), g is the acceleration due to gravity (cm s^{-2}), σ_p and σ_f are the density of the particle and the fluid (g cm^{-3}), respectively, and η is the dynamic viscosity of the fluid (g $cm\ s^{-1}$; Aylor 2002; Di-Giovanni et al. 1995). Although Stokes's law assumes that particles are rigid, smooth, and spherical, it is still considered to be an appropriate method for estimating the rate of settling of pollen grains that may be ornamented or irregularly shaped (Di-Giovanni et al. 1995).

Previous research has demonstrated that glyphosate resistance in Palmer amaranth can be transferred through pollen (Sosnoskie et al. 2007). The combined effects of pollen-mediated gene flow, genetic mutation, and continued intense selection pressure from glyphosate could precipitate the widespread accumulation of an adaptive glyphosate-resistance trait throughout the range of Palmer amaranth. In addition, the potential for hybridization among *Amaranthus* species has been demonstrated (Tranel et al. 2002; Trucco et al. 2005b) and could lead to the transfer of herbicide resistance by pollen to other pigweed species. The goal of this research is to describe the processes that influence the pollen-mediated dispersal of glyphosate resistance in Palmer amaranth, with the ultimate intention of developing a predictive model of pollen transport. The objective of this study was to describe the physical characteristics of Palmer amaranth pollen that affect its dispersal potential.

Materials and Methods

Fresh pollen was collected from multiple Palmer amaranth plants at the USDA-ARS Jones Farm in Tifton, GA, for 6 d in July and August in 2007. Pollen collections were made between 9:00 and 11:00 A.M., as the anthers presented and began to dehisce. Pollen grains were released from the anthers by gentle tapping or shaking of the main stem of the plant just below the inflorescence. Pollen samples were collected on aluminum foil, sieved (250-μm mesh opening) to remove large floral material, and transported within 30 min to the lab, where they were stored at 95 to 100% relative humidity (RH) in a polyvinyl container until use.

Samples of the harvested Palmer amaranth pollen were viewed at ×400 magnification with a light microscope.[1] Pollen diameter measurements (300 grains per sample) were made from images captured with a digital[2] camera with image analysis software.[3] The diameter distribution of the pollen grains was also determined with an electronic particle sizer.[4] The density of the solid material in dried pollen (48 h at 30 C) was determined with the use of a gas pycnometer[5] (Harrington and Metzger 1963; van Hout and Katz 2004).

A distribution of theoretical V_s for Palmer amaranth pollen was developed with the use of the results from the pollen diameter and density studies to parameterize Stokes's equation (Equation 1). It was assumed that the standard conditions for air at 30 C would be applied, therefore σ_f was 1.184 kg m^{-3}, and η was 1.89×10^{-5} kg $m\ s^{-1}$. The force of gravity was 9.81 m s^{-2}. The predicted distributions of Palmer amaranth pollen V_s were fit using a Gaussian function. In addition, the Reynolds number (Re) associated with each predicted settling velocity was also calculated (Hinds 1999; Reist 1984). The Reynolds number is a dimensionless parameter that describes the flow of a fluid around an object. It represents the ratio of inertial to viscous forces as a fluid moves around an obstacle and serves as a benchmark for determining whether flow is laminar or turbulent. Mathematically, the Reynolds number is defined as:

$$\mathrm{Re} = \frac{2rV\sigma_f}{\eta}, \quad [2]$$

where V is the relative velocity (cm s^{-1}) between the particle and the fluid (Hinds 1999; Reist 1984). When $\mathrm{Re} < 1$, viscous forces dominate, and the flow around the object is laminar (also known as Stokes flow). When $\mathrm{Re} > 1{,}000$, inertial forces are predominant, and the flow is said to be turbulent. For values between 1 and 1,000, flow is said to be intermediate. Stokes's law is valid only when laminar flow exists.

Empirical measurements of Palmer amaranth pollen settling velocity in still air were made with the use of a settling tower (Figure 1) modeled on a design by Di-Giovanni et al. (1995). The tower consisted of two clear polycarbonate tubes placed over a 5.1-cm-diam opening in a wooden box. The outer tube (25.4-cm diam × 174.0-cm length) completely encircled the inner tube (15.2-cm diam × 174.0-cm length) and insulated it from temperature gradients and resulting convective currents that could affect the settling of small particles. The top of the settling tower was sealed with a Plexiglas cap that had eight 6-mm-diam apertures (for holding pollen samples) positioned over the inner tube. Pollen samples were released into the inner chamber of the tower when a sliding plate under the apertures was removed. Inside the wooden box was a wooden, 50.8-cm-diam disk that rotated about its center with the use of a motor and gearbox assembly. Pollen was captured on petroleum-jelly–covered, glass microscope slides (5.0-cm length × 2.5-cm width) that were positioned 5.1 cm apart around the periphery of the rotating disk. The disk was aligned such that the center of each microscope slide would pass under the opening at the base of the settling tower as the disk turned. The disk rotation was regulated by a datalogger and controller,[5] which could be programmed to start the motor at any predetermined time (e.g., at pollen release, 10 s after pollen release, etc.). Changing the time delay enabled a change in the range of V_s observed. The settling velocity associated with each individual slide was a function of the position of a slide on the disk, the drop height, the speed with which the disk rotated (2.7 cm s^{-1}), and the time delay between pollen release and the start of the disk's rotation. Grains on the first slides that pass under the settling tower chamber have faster V_s than grains on the last slides. The performance of the settling

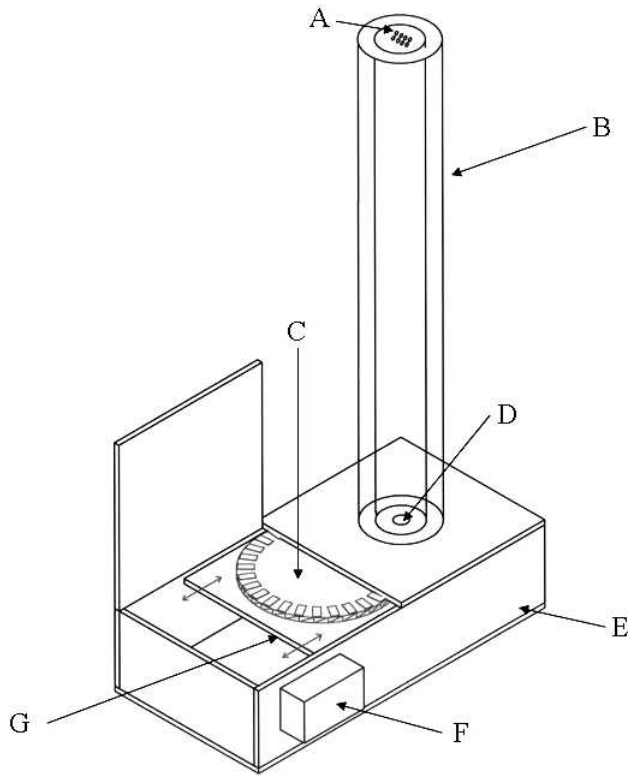

Figure 1. Diagram of the settling tower. A = apertures; B = insulated polycarbonate settling chamber; C = wooden rotating disk with slides; D = opening from the settling chamber to disk and slides; E = wooden chamber housing disk and gear box assembly; F = Campbell controller; G = sliding tables supporting disk.

tower was assessed with the use of freshly harvested corn pollen. The observed mean V_s for a sample of corn pollen with a mean diameter of 92.6 μm was 24.9 cm s^{-1}. These results are similar to those of Aylor (2002), who reported that the observed mean V_s for two hybrid varieties (90.7- and 91.3-μm diam) and one inbred line (93.4-μm diam) varied from 26.0 to 27.4 cm s^{-1}. Considering these results, we believe that the settling tower was sufficiently accurate and appropriate for use in this study.

The settling velocity studies were begun within 1 h of pollen harvest. Two runs were conducted each day. Before each run, a chemical static reducer was wiped throughout the inside of the inner tube to ensure that pollen grains did not stick to the walls. Pollen samples (35 mg) were loaded into the apertures at the top of the tower, released, and captured on the greased microscope slides. The rotating disk was programmed to start turning after a delay of 10 s; the V_s values represented by the slides ranged from 3.2 to 15.5 cm s^{-1}. Preliminary observations indicated that the majority of the pollen would settle between these rates (data not shown). Pollen counts were begun immediately after the conclusion of each run. All of the single pollen grains observed along two longitudinal sweeps of each slide at ×100 magnification were counted and recorded. Pollen grains within one pollen diameter of another grain were considered to be part of a grain cluster (≥ 2 pollen grains) and were recorded separately (Di-Giovanni et al. 1995). Because each individual slide represented a different settling speed, a frequency distribution of pollen V_s was constructed. Data for single pollen grains and grain clusters for each slide were converted to a percentage of the total number of dispersal units (single pollen grains plus grain clusters) observed over the entire run (Di-Giovanni et al. 1995). Replicates from the same day were averaged. Because the initial results suggested that the presence of pollen clusters was affecting the V_s of the single grains, the study was modified and repeated. In an attempt to eliminate pollen clusters, the pollen samples were passed through a Number 200 U.S. standard sieve (74-μm mesh opening) as they were introduced into the settling tower. The predicted distributions of Palmer amaranth pollen V_s were fit with the use of a Gaussian function.

Results and Discussion

Fully hydrated Palmer amaranth pollen grains are spheroidal and consistently pantoporate (i.e., with rounded apertures covering the surface; Borsch 1998; Franssen et al. 2001; Tsukada 1967). There were no differences in pollen size among days. Mean Palmer amaranth pollen diameter, as determined with the use of light microscopy, was 30.7 μm (± 2.34). This value is approximately 15% larger than the value (26.8 μm ± 4.31) obtained with the use of the particle sizer, and may represent unintentional bias toward the selection of larger, more robust pollen grains during the visual analyses. Pollen diameters ranged from 21 to 38 μm for the visually estimated samples and from 21 to 35 μm for the samples evaluated with the use of the particle sizer. The results obtained with the particle sizer agree with those of Vaissière and Vinson (1994), who, using an electronic particle analyzer, determined that the mean equivalent spherical diameter of dehydrated Palmer amaranth pollen was 26.3 μm. Similarly, Durham (1946) reported that the mean pollen diameter was 25.8 μm. These results vary considerably from those of Franssen et al. (2001), who reported that the mean pollen diameter for Palmer amaranth, as determined by scanning electron microscopy (SEM), was 19.8 μm. Pollen grain size can vary widely within and among plants and populations and is a function of both internal (ploidy level) and external (water, temperature, mineral nutrition) factors (Muller 1979). Another possible explanation for the observed differences in mean diameter is the timing of pollen collection. We collected loose pollen from naturally dehiscent anthers, whereas Franssen et al. (2001) collected from unopened flower buds. Preliminary investigations indicated that pollen grains harvested from immature flowers were smaller and cytologically less developed than shed pollen (data not shown). The dissimilarity between the results could also be due to the microscopy methods (light microscopy vs. SEM) used for visualizing the pollen. According to van Hout and Katz (2004), the mean diameter of dry corn pollen observed with the use of SEM (71.2 μm) was approximately 10% and 20% smaller than the mean diameters of dry (81.8 μm) and hydrated (89.2 μm) pollen, respectively, as measured by optical microscopy. They argued that the processes required to prepare samples for SEM viewing, which are conducted in a vacuum, fully evacuated residual air pockets in the dried pollen, thereby shrinking the grains further (van Hout and Katz 2004).

The mean density of the solid portion of Palmer amaranth pollen was 1,435 (± 3.9) kg m^{-3}. Mature Palmer amaranth pollen is approximately 7.5% starch (Roulston and Buchmann 2000), which has a density of 1,500 kg m^{-3}.

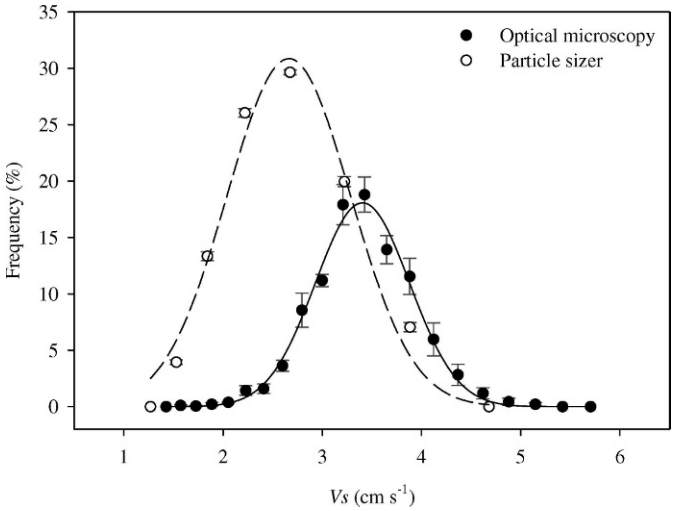

Figure 2. Frequency distributions of theoretical Palmer amaranth pollen V_s developed with the use of two pollen diameter distributions that were determined by optical microscopy and an electronic particle sizer. The distribution of V_s developed with the optical microscopy data represents the mean of six replicates of 300 pollen grains each. The distribution of V_s developed with the particle sizer data represents the mean of four replicates of at least 10,000 pollen grains each:

$$y_{\text{optical}} = 18.0 \exp\left[-0.5\left(\frac{x - 3.4}{0.5}\right)^2\right]; \quad R^2 = 0.89.$$

$$y_{\text{sizer}} = 30.9 \exp\left[-0.5\left(\frac{x - 2.7}{0.6}\right)^2\right]; \quad R^2 = 0.97.$$

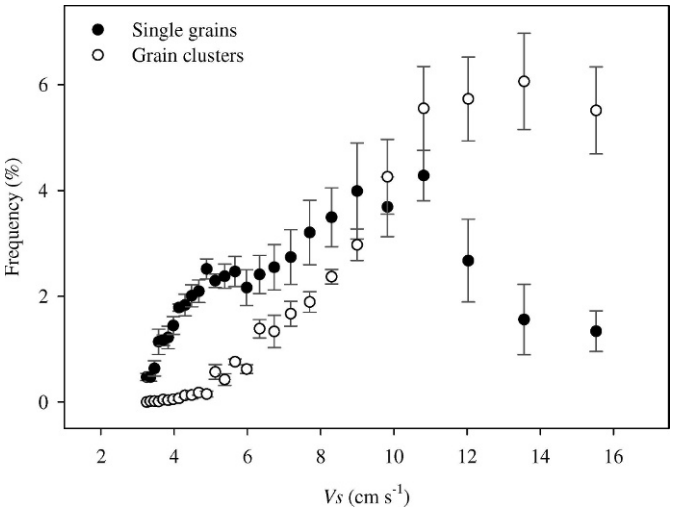

Figure 3. The distribution of empirically determined Palmer amaranth pollen V_s values without an additional sieving procedure. Single grains were scored as individual pollen grains that were separated from other grains by at least one pollen diameter. Grain clusters were pollen grains that were less than one pollen diameter from neighboring grains. Each point is the mean of six series of runs carried out over 6 d in July and August of 2007. An average of 498 and 310 single pollen grains and grain clusters, respectively, were observed during each run across all V_s.

Corn pollen, which is greater than 30% starch, has a mean density of 1,450 kg m^{-3} (Aylor 2002). Assuming that there are no substantial air pockets present within the dehydrated pollen grains (Harrington and Metzger 1963; van Hout and Katz 2004), the density of fresh pollen can be described as the weighted average of the densities of the solid and aqueous fractions. Niklas (1985) reported that the density of cellular protoplasm does not vary considerably among species and is roughly equal to the density of water (1,000 kg m^{-3}). Preliminary studies indicated that Palmer amaranth pollen grains are at least 50% water (data not shown); therefore, the density of fresh pollen was estimated to be 1,218 kg m^{-3}.

Stokes's law was used to determine the distribution of theoretical V_s for single, fully hydrated Palmer amaranth pollen grains (Figure 2). For a distribution of pollen diameters ranging from 21 to 38 μm with a mean of 30.7 μm, as determined with the use of light microscopy, the theoretical V_s ranged from 1.6 to 5.1 cm s^{-1}, with a mean of 3.4 cm s^{-1}. For a distribution of pollen diameters ranging from 21 to 35 μm with a mean of 26.8 μm, as determined with the use of a particle sizer, the theoretical V_s ranged from 1.5 to 3.8 cm s^{-1}, with a mean of 2.6 cm s^{-1}. Approximately 75% of the V_s within a given distribution were within one standard deviation of their respective means. The associated Reynolds numbers never exceeded 0.12, indicating laminar flow around the grains (Hinds 1999; Reist 1984).

Figure 3 shows the observed distribution of V_s for Palmer amaranth pollen. The V_s for single pollen grains ranged from 3.2 to 15.5 cm s^{-1}. A visual examination of the data revealed that the V_s distribution was roughly bimodal; one mode was located at 5.0 cm s^{-1} and the other at 10 cm s^{-1}. The second mode appears to be associated with the distribution of V_s for grain clusters (≥ 2 pollen grains), and it is presumed to depict the V_s of individual grains with rates of settling that have been altered because of the larger, faster-settling aggregates (Aylor 2002; Di-Giovanni et al. 1995). According to Reist (1984), the movement of an object in a fluid will reduce the resistance of that fluid to other nearby objects, thereby increasing their V_s. Although particle–particle interactions are usually negligible because the spacing among objects is quite large relative to the size of the objects, it is not unreasonable to assume that the presence of clusters skewed the distribution of V_s for single grains toward the faster values (Durham 1946; Ferrandino and Aylor 1984). Alternately, it is also possible that the single pollen grains settling at the faster V_s were not just influenced by the presence of pollen clusters, but were actually components of those same clusters that became separated from the main unit during settling or upon impact.

The entire study was repeated with the intention of isolating and observing just single pollen grains. To minimize the influence of pollen aggregates, pollen samples were passed through a sieve as they were introduced into the settling tower. This additional step succeeded in reducing the occurrence of the larger pollen masses. For the first run of the study (without additional sieving), pollen clusters accounted for 38% of all of the observed dispersal units, whereas for the second run of the study (with additional sieving), clusters represented only 13% of the total number of dispersal units (data not shown). The mean V_s for sieved single pollen grains was 5.0 cm s^{-1}, although there is some indication that clumps could still be affecting V_s (Figure 4). There were several extreme observations that occurred at 5.4 cm s^{-1}, 5.7 cm s^{-1}, and 6.0 cm s^{-1} that skewed the frequency distribution for individual pollen grains. Most of the observed pollen clusters settled between 5.4 and 6.3 cm s^{-1}. If these outliers are removed from the analysis, the mean V_s for individual grains is 4.5 cm s^{-1}. It is unclear if Palmer amaranth pollen grains become aggregated in the

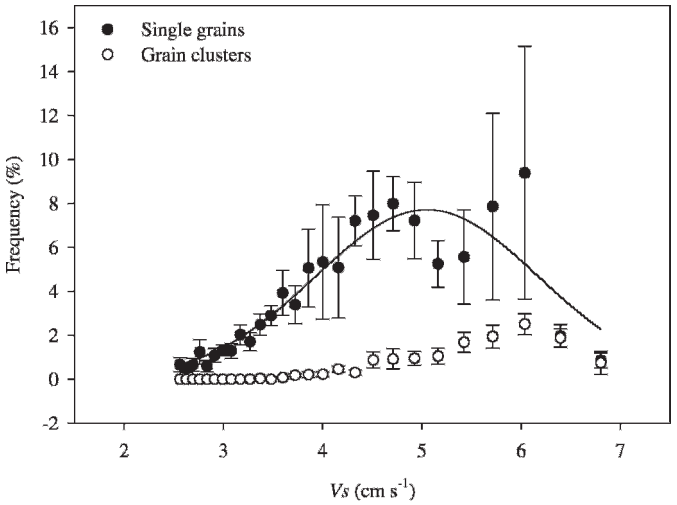

Figure 4. The distribution of empirically determined Palmer amaranth pollen V_s values following an additional sieving procedure. Single grains were scored as individual pollen grains that were separated from other grains by at least one pollen diameter. Grain clusters were pollen grains that were less than one pollen diameter from neighboring grains. Each point is the mean of six series of runs carried out over 6 d in July and August of 2007. An average of 420 and 67 single pollen grains and grain clusters, respectively, were observed for each run across all V_s:

$$y = 7.7 \exp\left[-0.5\left(\frac{x - 5.0}{1.1}\right)^2\right]; \quad R^2 = 0.36.$$

environment or if this phenomenon is an artifact of the experiment. Unlike Di-Giovanni et al. (1995) and Ferrandino and Aylor (1984), no attempt was made to characterize the settling of larger dispersal units. Even if clusters are naturally occurring, it is unlikely that they contribute significantly to long-distance dispersal, because of their high V_s. The continuing disparity between the estimated and the observed V_s values may be due, in part, to the changing physical nature of shed pollen grains. Stokes's law assumes that particles maintain a constant shape, size, and density. As Palmer amaranth pollen desiccates, the grains consistently assumed a deflated, bowl-like shape. Based on visual observations, the majority of Palmer amaranth pollen grains appeared to fall convex-side down (data not shown); a hemisphere that falls in this manner has a lower drag coefficient (Hoerner 1965) than does a sphere, and is presumed to settle more quickly. Durham (1946) reported that the mean empirical V_s of Palmer amaranth pollen in still air was 1.9 cm s^{-1}. This is 27 and 44% slower than the theoretical estimates of 2.6 and 3.4 cm s^{-1}, and 61% slower than the observed estimate of 5.0 cm s^{-1} presented in this article. According to Jackson and Lyford (1999), Durham's estimates of V_s are consistently lower than the estimates of others working with either the same or similar species. For example, Durham's mean V_s (18.0 cm s^{-1}) for corn pollen (90.0-µm diam) is greater than 27% smaller than the means reported by Bodmer (1922; 26.0 cm s^{-1}), Aylor (2002; 90.7 to 93.4–µm diam, 26.0 to 27.4 cm s^{-1}), and the current study (92.8-µm diam, 24.9 cm s^{-1}).

The impetus for this study was the rapid development of glyphosate resistance in Georgia Palmer amaranth populations (Culpepper et al. 2006). Currently in Georgia, there exist known Palmer amaranth populations resistant to only glyphosate and ALS-inhibiting herbicides (Culpepper et al. 2006; Heap 2008). However, this species has documented resistance to the triazine and dinitroaniline herbicides in other states (Gossett et al. 1992; Heap 2008; Peterson 1999), and a closely related species, tall waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer], has developed resistance to all of these herbicide classes as well as the protoporphyrinogen oxidase (PPO) –inhibiting herbicides (Legleiter and Bradley 2008; Patzoldt et al. 2005). The PPO-inhibiting herbicides are the primary herbicide options to control glyphosate-resistant Palmer amaranth in glyphosate-resistant cotton (Culpepper et al. 2008). Therefore, a better understanding of pollen-flow dynamics and the mechanisms by which herbicide resistance traits can be exchanged between populations will allow the monitoring of suspect populations and improve scouting strategies in areas in proximity to identified herbicide-resistant populations. Pollen-mediated gene flow from herbicide-resistant crops to wild relatives has been investigated for many species (Marshall et al. 2001; Messeguer et al. 2004; Warwick et al. 2008; Wilkinson et al. 2003); however, there have been fewer studies that have evaluated transfer of traits among weedy species, with many of those focused on interspecific crosses (Franssen et al. 2001; Tranel et al. 2002; Wetzel et al. 1999). This area of research will likely become more important in the development of weed management systems as more wind-dispersed species evolve herbicide resistance.

Sources of Materials

[1] Light microscope, Olympus BH2, Olympus America, Inc., Center Valley, PA 18034.

[2] Digital camera, SPOT Insight, Diagnostic Instruments, Inc., Sterling Heights, MI 48314.

[3] Image analysis software, SPOT Advanced, Diagnostic Instruments, Inc., Sterling Heights, MI 48314.

[4] Electronic particle sizer, Beckman Coulter LS 13 320, Beckman Coulter, Inc., Fullerton, CA 92834.

[5] Gas pycnometer, Campbell Scientific 21× Datalogger and Controller, Campbell Scientific, Inc., Logan, UT 84321.

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